

A SUMMARY OF EXPERIMENTAL HYBRIDIZATION IN VERBESINA (COMPOSITAE)¹

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Verbesina, a genus of approximately 250 species, ranges from southern Canada into Argentina and has its greatest concentration of species in Mexico and Central America. During the past decade, I have published papers on the experimental hybridization of the United States species (Coleman, 1968, 1971, 1974). The object of this paper is to present information on previously unreported experimental F₁ hybrids and to synthesize and summarize the results of the experimental hybridization program.

The cytological methods employed are essentially those given in the previously cited papers. Collection sites for the parent plants used in the production of the newly reported F₁s are as follow: *Verbesina alternifolia* (L.) Britton ex Kearney, Clarke Co., Ga., Izard Co., Ark., and Montgomery Co., Md.; *V. aristata* (Ell.) A. Heller, Holmes Co., Fla.; *V. glabrata* H. & A., São Paulo, Brazil; *V. helianthoides* Michx., Sumter Co., Ala.; *V. heterophylla* (Chapman) A. Gray, Baker Co., Fla.; *V. lindheimeri* Rob. & Greenm., Blanco Co., Tex.; *V. microptera* DC., San Patricio Co., Tex.; *V. occidentalis* (L.) Walt., Clarke Co., Ga.; *V. rothrockii* Rob. & Greenm., Cochise Co., Ariz.; *V. virginica* L. (typical variety), Forest Co., Miss. and Poinsett Co., Ark.; *V. virginica* L. var. *laciniata* (Poir.) A. Gray, Taylor Co., Fla.; *V. walteri* Shinnery, Allen Parish, La. All parental material showed very regular bivalent formation and pollen stainability, taken as a measure of male fertility, averaged above 85% in each case. Each species is diploid, $n = 17$, with the exception of *V. alternifolia*, which is tetraploid, $n = 34$.

Figure 1 presents a crossing diagram and summarizes those crosses which failed to result in F₁s; Figure 2 presents a crossing diagram summarizing those crosses which resulted in F₁s. Only species of the United States are included in the diagrams. Figures 3-12 present representative leaves of some of the species, and Figures 13-21 present representative leaves of some F₁s. Voucher material has been retained by the author.

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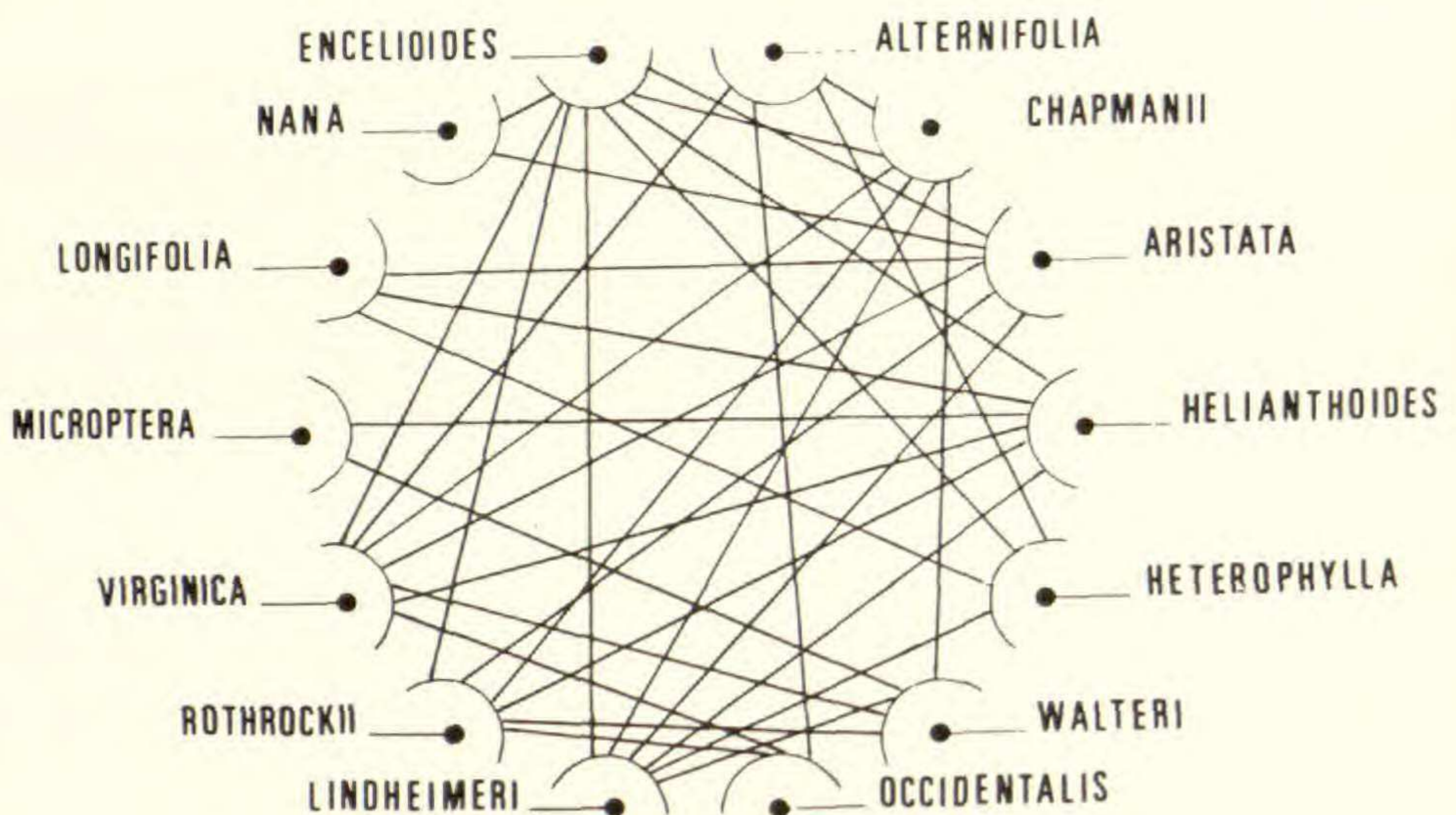


Figure 1. Diagram indicating crosses between United States species of *Verbesina* that failed to yield F_1 hybrids.

NEW HYBRIDS

***Verbesina aristata* × *V. glabrata*.** Two plants were involved in this cross, and 3.5% of the 230 florets crossed formed full achenes. Two robust F_1 s were obtained which had 1% and 7% pollen stainability. Chromosomes in the hybrids were sticky, and the five analyzable cells obtained showed 72% of the chromosomes associated in bivalents.

Verbesina glabrata reaches heights of 3–5 m and has oblanceolate leaves which frequently reach 20 cm in length and 5 cm in width. *Verbesina aristata* is generally less than 70 cm tall and has elliptic to elliptic-oblong leaves (Figure 3) mostly less than 8 cm long and 3 cm wide. The F_1 s were nearly 1 m tall, with leaves tending toward those of *V. glabrata* in shape but toward those of *V. aristata* in size. Geographically, this is the widest cross achieved in *Verbesina*. *Verbesina glabrata* is a wide-ranging Brazilian species, whereas *V. aristata* is restricted to adjacent regions of Alabama, Georgia, and Florida.

***Verbesina heterophylla* × *V. occidentalis*.** Two plants were involved in this cross, and 21% of the 205 florets crossed formed full achenes. The five F_1 s were vigorous, but highly sterile with no plant having greater than 2% pollen stainability. One hundred and three cells of three F_1 s were analyzed, and 28% of the chromosomes were associated in bivalents.

Verbesina heterophylla is mostly 50–70 cm tall, while *V. occidentalis* commonly exceeds 1.5 m. The F₁s were 80–95 cm tall. The leaves of *V. heterophylla* (Figure 4) are generally elliptic-oblong, 4–8 cm long, 2–3 cm wide, scabrous, and sessile. Those of *V. occidentalis* (Figure 5) are ovate, frequently exceed 20 cm in length and 8 cm in width, and are smooth and petiolate. Leaf shape of the F₁s (Figure 13) tended toward *V. occidentalis*, whereas leaf length was nearer to that of *V. heterophylla*. Roughness was intermediate, while the petiolate condition tended toward *V. occidentalis*. *Verbesina heterophylla* is restricted to the northeastern region of Florida, an area in which *V. occidentalis* is poorly represented, if it occurs at all.

***Verbesina virginica* × *V. heterophylla*.** Six crossing combinations were made, and 1.4% of the 701 florets crossed formed full achenes. The single F₁ obtained was essentially fully sterile. Sixty-seven cells were analyzed, and 36% of the chromosomes were associated in bivalents.

Verbesina virginica frequently exceeds 1.5 m, whereas *V. heterophylla* is mostly less than 70 cm tall. The petiolate, ovate leaves of *V. virginica* (Figure 7) commonly attain 15 cm in length and 7 cm in width. The sessile, elliptic-oblong leaves of *V. heterophylla* (Figure 4) are mostly less than 8 cm long and 3 cm wide. The F₁ was intermediate in height with petiolate leaves which tended in shape toward those of *V. virginica* and approached those of that species in size (Figure 14). *Verbesina virginica* commonly has more than 100 heads per shoot, whereas those of *V. heterophylla* generally have many fewer than 20. Floret color is white in *V. virginica* and yellow in *V. heterophylla*. The F₁ had about 80 heads and white florets with some pinkish coloration. Both species occur in northeastern Florida and, although I have never seen a mixed population, it is possible that the species occur in sufficient proximity to permit intercrossing in nature.

***Verbesina lindheimeri* × *V. rothrockii*.** Four crossing combinations were made, and 28% of the 496 florets crossed formed full achenes. Five vigorous F₁s were grown, and the single plant checked showed 77% pollen stainability. A study of 36 cells of three hybrids revealed 99% of the chromosomes associated in bivalents.

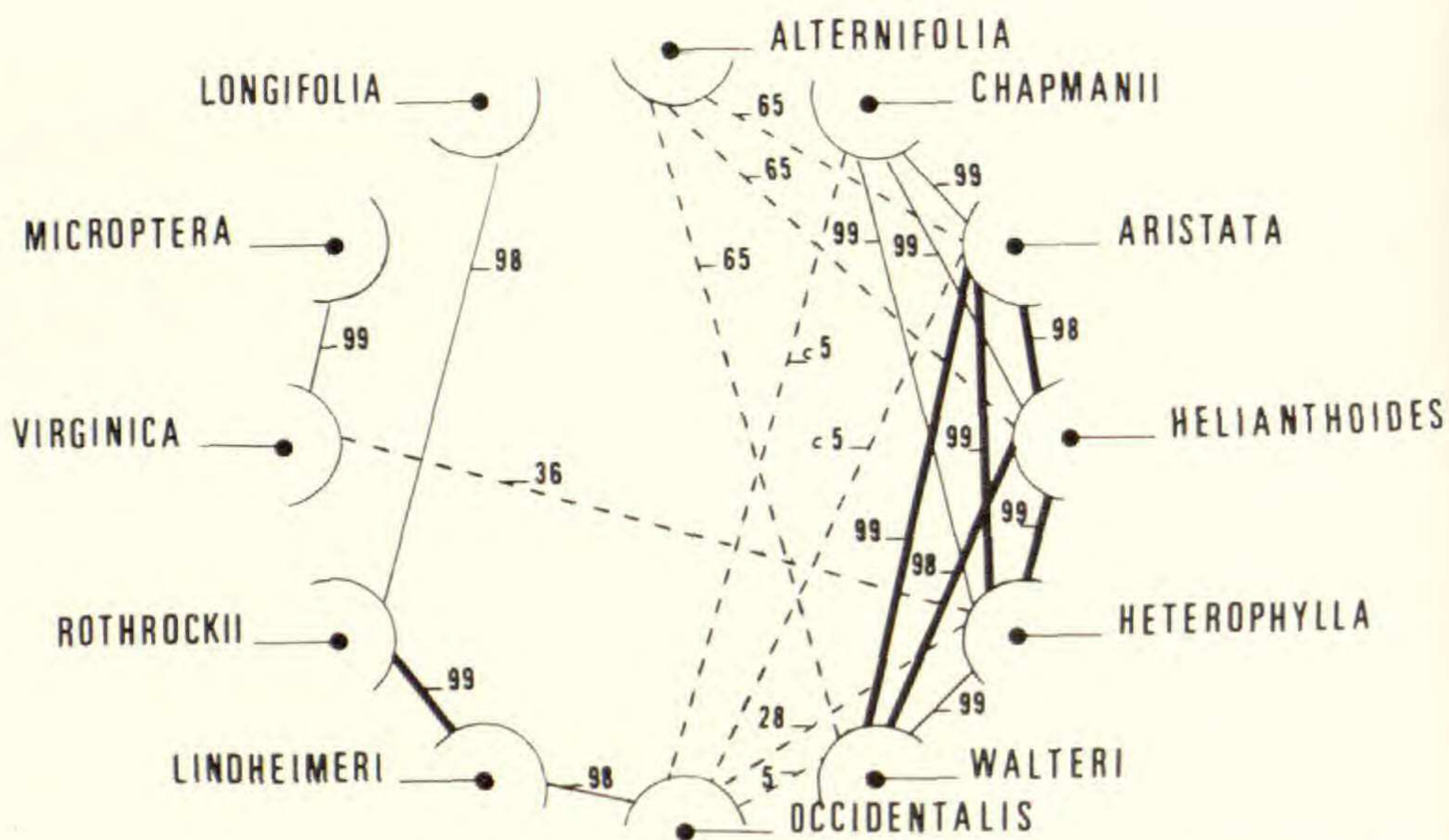


Figure 2. Diagram indicating crosses between United States species of *Verbesina* resulting in F_1 hybrids. Broken lines indicate F_1 hybrids with mean pollen stainability of 0%-20%, thin lines 45%-72%, and heavy lines 77%-99%. The number along the line is the percentage of F_1 chromosomes associated in bivalents, the remaining occurring as univalents.

Although readily separable, these species demonstrate a close morphological affinity. *Verbesina lindheimeri* has ovate, non-auriculate leaves (Figure 6) which frequently exceed 10 cm in length and 6 cm in width, whereas *V. rothrockii* has oblong or lance-oblong, mostly auriculate-based leaves, rarely to 9 cm in length and 4 cm in width. The F_1 s were strongly intermediate. These species are allopatric. *Verbesina rothrockii* ranges from southern Arizona and southern New Mexico across northern Mexico, whereas *V. lindheimeri* is endemic to southcentral Texas.

***Verbesina lindheimeri* × *V. occidentalis*.** Two plants were involved in the crossing, and 5.6% of the 244 florets crossed formed full achenes. The three vigorous F_1 s had pollen stainability of 46%, 48%, and 62%, and the 83 cells studied revealed 98% of the chromosomes associated in bivalents.

Leaves of *Verbesina occidentalis* commonly exceed 20 cm in length, and are thin and smooth (Figure 5). *Verbesina lindheimeri* has leaves mostly less than 15 cm long which are thicker and strongly scabrous (Figure 6). Leaves of the F_1 s (Figure 15) were intermediate in all respects. Flowering heads of *V. occidentalis* have mostly 2-4 rays and head diameter, less rays, is generally less than

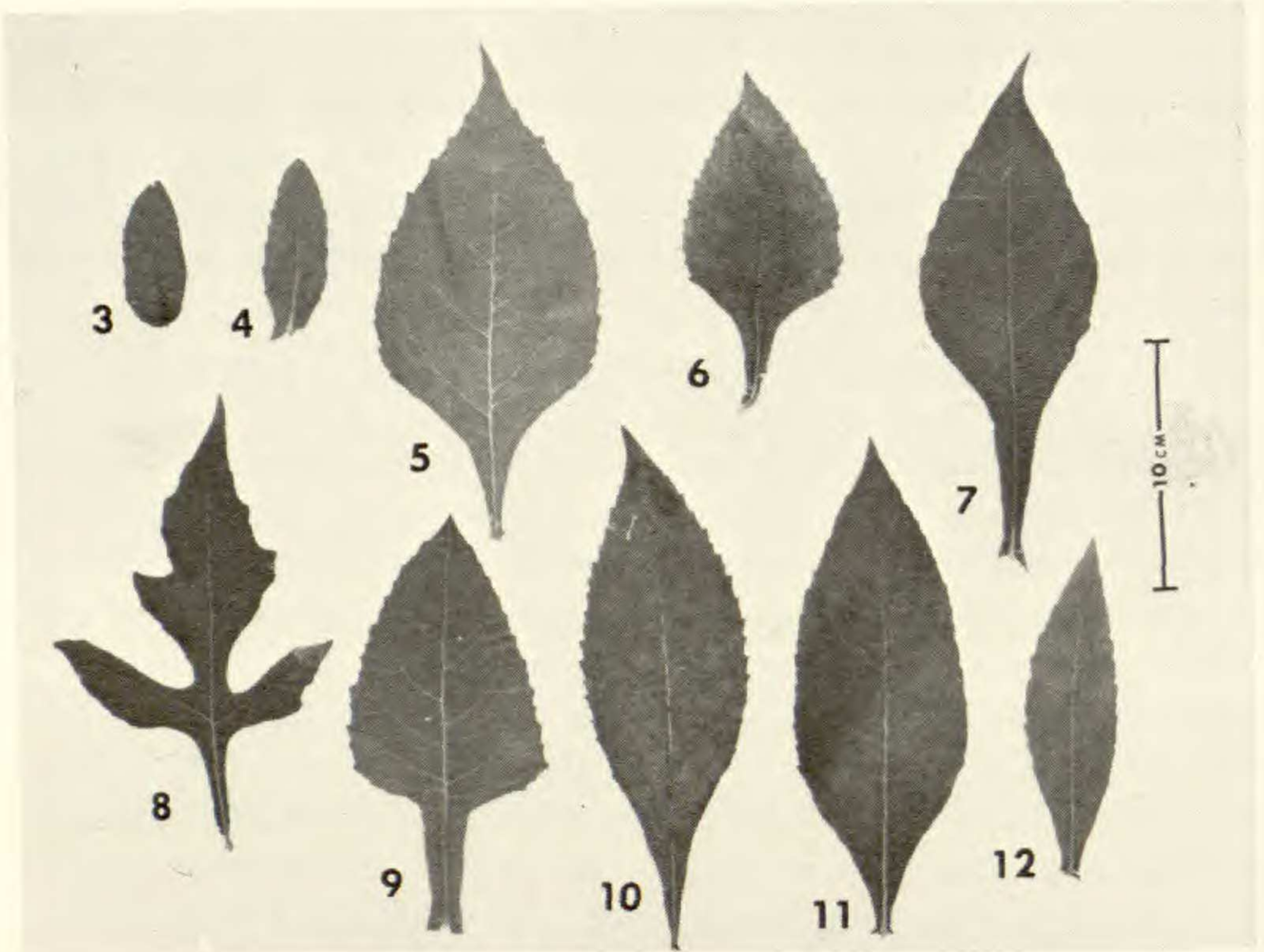
1 cm. *Verbesina lindheimeri* has mostly 10–12 rays per head, and head diameter, less rays, is mostly greater than 2 cm. The F_1 s were intermediate for ray number and head size. These species are allopatric. *Verbesina lindheimeri* is endemic to southcentral Texas, whereas *V. occidentalis* is found throughout much of the eastern one-third of the country.

CROSSES WITHIN THE VERBESINA VIRGINICA COMPLEX

Verbesina virginica is a tall, white-flowered species common from Kansas to South Carolina and southward. The leaves are typically ovate with subentire to merely toothed margins (Figure 7). However, from coastal South Carolina into Florida they are frequently sinuately to deeply lobed (Figure 8) or, rarely, dissected. Since intergradation occurs between the various leaf forms, the lobe-leafed populations are usually treated as a variety, var. *laciniata* (Poir.) A. Gray, but have also been considered as a distinct species, *V. laciniata* (Poir.) Nutt. Two recent floras of the Southeast differ in their treatments. Radford, Ahles, and Bell (1964) treat the lobe-leafed form as a variety, while Long and Lakela (1971) treat it at the specific level.

Verbesina virginica typically has 1–5 rayed heads with distinct gaps occurring between the rays. However, populations clearly related to *V. virginica* occur in southern coastal Texas and adjacent Mexico and have mostly 10–12 rays per head, resulting in a more closed circle of rays. Some of these populations also have more deltoid leaves (Figure 9) and more numerous flowered heads than does typical *V. virginica*. These populations are generally accepted as a distinct species, *V. microptera* DC. However, Gray (1883) considered them conspecific with *V. virginica*, and Correll and Johnston (1970), while treating them as *V. microptera*, suggest their inclusion in *V. virginica*.

Crosses were made utilizing plants of two typical populations, one from Forest Co., Miss., and the other from Poinsett Co., Ark., a lobe-leafed population from Taylor Co., Fla., and a southern Texas population from San Patricio Co. A total of 23 plants was involved in the crossing. Mean achene set was fairly high for each cross, ranging from 30%–54%, and vigorous F_1 s were obtained in each case. Mean F_1 pollen stainability was as follows: Miss. × Ark., 95% for five plants; Fla. × Miss., 93% for six plants; Tex. × Ark., 73% for seven plants; Tex. × Fla., 41% for twelve plants;



Figures 3-12. Representative leaves of some species of *Verbesina*. 3, *V. aristata*; 4, *V. heterophylla*; 5, *V. occidentalis*; 6, *V. lindheimeri*; 7, *V. virginica* (typical variety); 8, *V. virginica* var. *laciniata*; 9, *V. microptera*; 10, *V. walteri*; 11, *V. alternifolia*; 12, *V. helianthoides*.

Tex. × Miss., 73% for nine plants. About 30 cells were studied for each group of F_1 s and, in each case, approximately 99% of the chromosomes were associated as bivalents. The hybrid nature of the F_1 s was readily evident, except for those between the typical populations, which were very similar morphologically. F_1 leaf shapes were intermediate between those of the parental populations, and the F_1 s formed with the Texas populations showed intermediacy in head size and ray number.

The close affinities suggested for these population systems on morphological grounds are substantiated by the close homology of their genomes and the generally high fertility of their F_1 s. The lobe-leaved populations of the Southeast are probably more practically viewed as a variety of *Verbesina virginica*, whereas the southern Texas populations, although closely allied to *V. virginica*, are probably deserving of specific status.

***Verbesina walteri* × *V. occidentalis*.** Six crossing combinations were made, and 13.7% of the 1042 florets crossed formed full achenes. The two F_1 s grown were weak, chlorotic, and fully sterile. The 51 cells analyzed showed 5% of the chromosomes associated as bivalents.

Verbesina occidentalis has smooth, opposite, broadly ovate leaves which commonly exceed 8 cm in width and are three-nerved from the base of the blade (Figure 5). Those of *V. walteri* are subscabrous, alternate, narrowly elliptic, lanceolate, or oblanceolate, mostly less than 5 cm wide and pinnately nerved (Figure 10). The alternate, pinnately nerved leaves of the F_1 s (Figure 16) were lance-elliptic to narrowly ovate, mostly less than 5 cm wide, and tended toward *V. occidentalis* in smoothness. The heads of *V. occidentalis* are elongate, rayed, and yellow-flowered, whereas those of *V. walteri* are globose, discoid, and white-flowered (Figure 22). Heads of the F_1 s were intermediate in shape with rays which were essentially greatly elongated disc florets (Figure 23). F_1 floret color was initially yellow, but quickly faded to pale yellow, then white. The species are sympatric in South Carolina, but natural hybrids are unknown.

***Verbesina alternifolia* × *V. helianthoides*.** Eleven crossing combinations were made, and 7.6% of the 2213 florets crossed developed full achenes. Successful crosses were obtained using *V. alternifolia* from Iazard Co., Ark. Three robust, but fully sterile, triploids were grown. A study of 33 cells showed mostly 34 bodies per cell, indicating the presence of 17 bivalents and 17 univalents. However, occasional cells with 32 or 33 bodies suggest the possibility of occasional trivalents.

Verbesina alternifolia mostly exceeds 1.5 m in height, has leaves commonly exceeding 15 cm in length (Figure 11), and has globose heads (Figure 24) frequently exceeding 50 per shoot. *Verbesina helianthoides* is mostly less than 1 m tall, with leaves less than 15 cm long (Figure 12), and has campanulate heads (Figure 25), generally fewer than 10 per shoot. The F_1 s were 70–80 cm tall, with the longest leaves to about 15 cm long (Figure 17), and had about 10 nearly globose heads per shoot. *Verbesina helianthoides* occurs from southwestern Ohio into northwestern Texas and is sympatric with *V. alternifolia* throughout most of its range. However, I know of no natural hybridization.

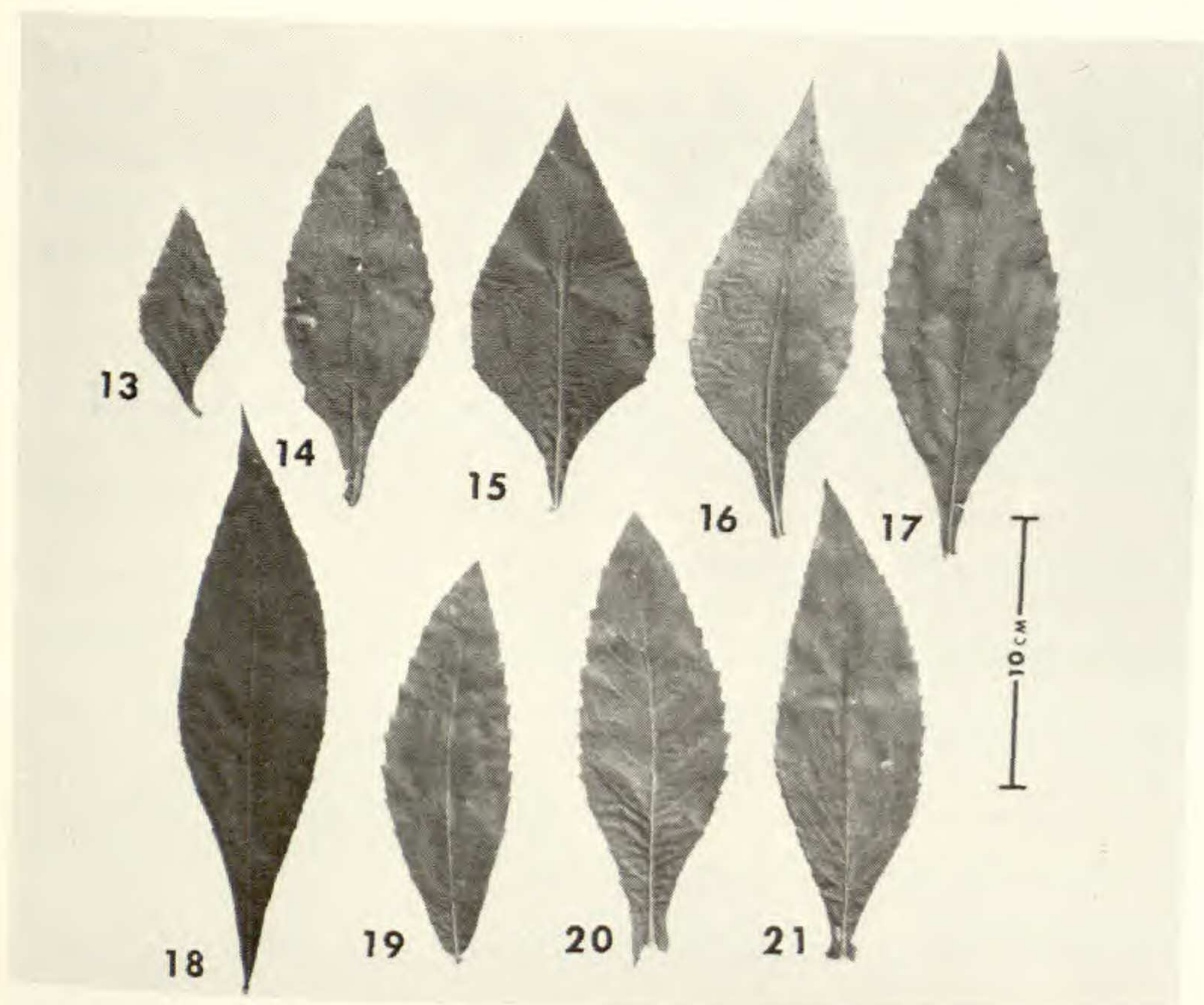
***Verbesina walteri* × *V. alternifolia*.** Ten crossing combinations were made, and 7.6% of the 2044 florets crossed formed full achenes. The 13 triploid F_1 s grown were vigorous but completely sterile. F_1 s resulting from crosses using *V. alternifolia* from Montgomery Co., Md., showed a complete failure of the meiotic process, whereas those produced using *V. alternifolia* from Clarke Co., Ga., produced abnormal, mostly non-staining pollen. The 18 cells analyzed showed mostly 34 bodies, indicating a prevalent pairing configuration of 17 bivalents and 17 univalents. Although no definite trivalents were observed, occasional cells showing 32 or 33 bodies suggest their possible occasional occurrence.

The principal morphological differences between these species are that *Verbesina walteri* has glabrous stems and white-flowered, discoid heads (Figure 22), whereas *V. alternifolia* has hirsute stems and yellow-flowered, rayed heads (Figure 24). The F_1 s were intermediate for stem pubescence and had rayed heads with the florets initially yellow, but fading to pale yellow, then white. Many rays had corolla tubes distinctly longer than pure *V. alternifolia*. F_1 leaf shape (Figure 18) tended toward *V. walteri*. These species occur sympatrically in Arkansas and possibly in Louisiana and the Carolinas, but natural hybrids are unknown.

THE HYBRID ORIGIN OF THE TETRAPLOID *VERBESINA ALTERNIFOLIA*

Verbesina alternifolia is one of the few tetraploid species reported for the genus. It and the closely related *V. walteri*, a diploid, have at times been separated to form the genus *Actinomeris* Nutt. These species share a combination of characters, globose heads and glaucous stems, not encountered elsewhere in the genus. Coleman (1971) demonstrated a close homology of the chromosomes of *V. walteri* and three unquestioned species of *Verbesina*, thereby supporting the inclusion of *V. walteri* and *V. alternifolia* in *Verbesina*.

In considering the parentage of *Verbesina alternifolia*, serious attention must be focused on *V. walteri* since this is the only extant species which could have contributed the combination of globose heads and glaucous stems. If *V. walteri*, which has white-flowered, discoid heads and glabrous stems, is in fact a genome donor to *V. alternifolia*, the second donor would be expected to have yellow-



Figures 13-21. Representative leaves of some interspecific F_1 *Verbesina* hybrids. 13, *V. heterophylla* \times *V. occidentalis*; 14, *V. virginica* \times *V. heterophylla*; 15, *V. lindheimeri* \times *V. occidentalis*; 16, *V. walteri* \times *V. occidentalis*; 17, *V. alternifolia* \times *V. helianthoides*; 18, *V. walteri* \times *V. alternifolia*; 19, *V. walteri* \times *V. aristata*; 20, *V. walteri* \times *V. heterophylla*; 21, *V. walteri* \times *V. helianthoides*.

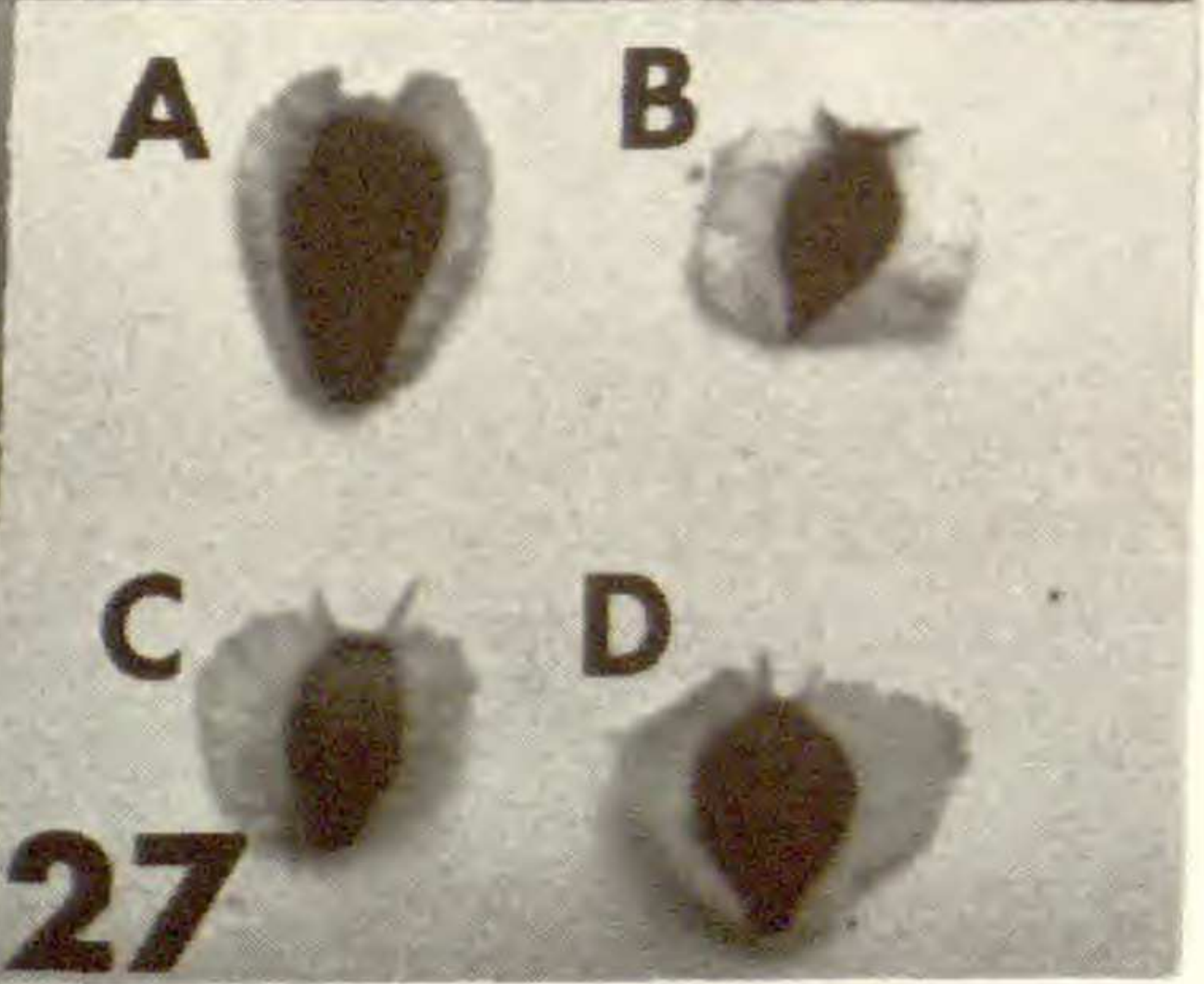
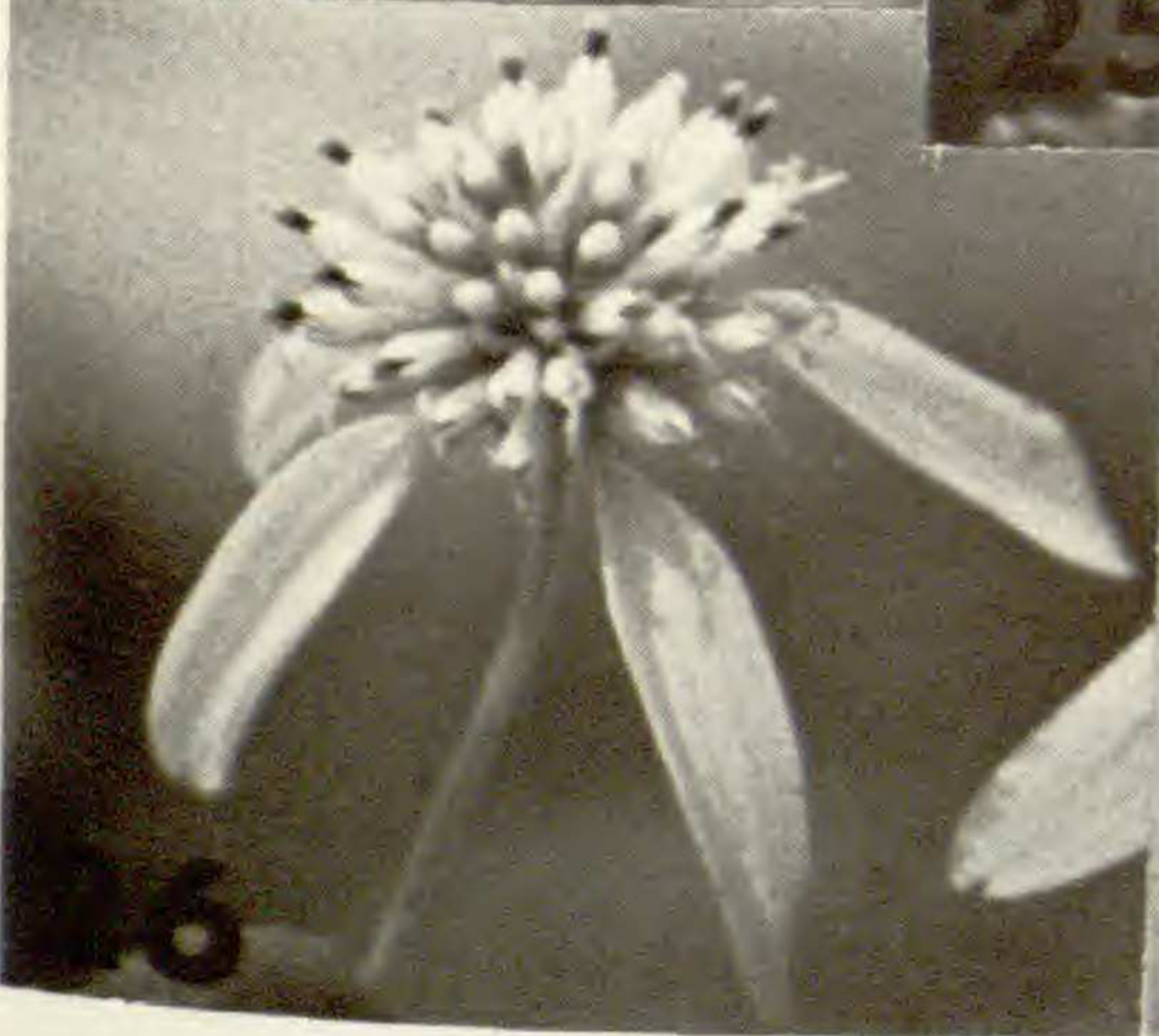
flowered, rayed heads and hirsute stems since these are the characters which best distinguish *V. alternifolia* from *V. walteri*. *Verbesina walteri* has been hybridized with three species having these characters: *V. aristata*, *V. heterophylla*, and *V. helianthoides* (Coleman, 1971). Leaves of the induced *V. walteri* \times *V. aristata* F_1 s (Figure 19) and the *V. walteri* \times *V. heterophylla* F_1 s (Figure 20) differ considerably from those of *V. alternifolia* (Figure 11). Furthermore, the stems of the *V. walteri* \times *V. aristata* F_1 s contrast with those of *V. alternifolia* by being wingless, and achene shape in the *V. walteri* \times *V. heterophylla* F_1 s differs strongly from that of *V. alternifolia*. However, the leaves of the induced *V. walteri* \times *V. helianthoides* F_1 s (Figure 21) compare favorably with those of *V. alternifolia* (Figure 11), as do head shape (Figures 24, 26), achene shape (Figure 27), stem pubescence, and most other charac-

teristics. *Verbesina helianthoides*, furthermore, is the only species of the three to occur sympatrically with *V. walteri*, and a natural *V. walteri* × *V. helianthoides* F₁ has been reported from Polk Co., Arkansas (Coleman, 1971). The principal morphological differences between *V. alternifolia* and the *V. walteri* × *V. helianthoides* F₁s are that F₁ floret color, although initially yellow, soon fades to pale yellow, then white, and the ray tubes are mostly longer than in *V. alternifolia*. Since the chromosomes of *V. walteri* and *V. helianthoides* are highly homologous, finely discriminatory preferential pairing would be essential for assuring fertility in doubled F₁s leading to the formation of *V. alternifolia*.

An additional diploid species, *Verbesina occidentalis*, has also been hybridized with *V. walteri*. *Verbesina occidentalis* satisfies the criteria of having rayed, yellow-flowered heads, but has glabrous or merely puberulent stems. The *V. walteri* × *V. occidentalis* F₁s compare well with *V. alternifolia* for leaf shape (Figures 11, 16), but differ in having much less pubescent stems, floret color fading to white, and by having mostly tubular rays which are essentially elongated disc florets (Figure 23). *Verbesina walteri* and *V. occidentalis* occur sympatrically in South Carolina, but I have never observed a natural F₁. Also, the induced F₁s were weak and chlorotic, and it is questionable whether natural F₁s could survive to maturity. The chromosomes of *V. walteri* × *V. occidentalis* are non-homologous, and preferential pairing of homologous genomes could be expected in doubled F₁s.

Both *Verbesina walteri* and *V. helianthoides* have been successfully crossed with *V. alternifolia*. In both cases the triploid F₁s exhibited mostly 17 bivalents and 17 univalents, suggesting that in each case the diploid genome was paired with one of the genomes of *V. alternifolia*. It cannot, however, be demonstrated whether the *V. helianthoides* and *V. walteri* genomes pair with the same or different genomes of *V. alternifolia*. It is also possible that the univalents in the triploids represent the diploid genomes, and that autosyndetic pairing occurs between the *V. alternifolia*

Figures 22-27. Flowering heads of some species and interspecific F₁ hybrids of *Verbesina*. 22, *V. walteri*; 23, *V. walteri* × *V. occidentalis*; 24, *V. alternifolia*; 25, *V. helianthoides*; 26, *V. walteri* × *V. helianthoides*; 27, achenes of *V. helianthoides* (A), *V. walteri* (B), *V. walteri* × *V. helianthoides* (C), and *V. alternifolia* (D).



genomes. However, the strong morphological evidence favoring the occurrence of the *V. walteri* genome in *V. alternifolia* tends to minimize this possibility.

The triploid hybrids provide genetic evidence that pale floret color in the *Verbesina walteri* × *V. helianthoides* F₁s is the result of dosage effect. Letting W represent the white allele of *V. walteri*, and w the yellow allele of *V. helianthoides*, and assuming an origin for *V. alternifolia* from the spontaneous doubling of the chromosome complement of *V. walteri* × *V. helianthoides* F₁s, the following plants would have the genotype given for the phenotype observed:

	Phenotype	Genotype
<i>V. walteri</i>	white	WW
<i>V. helianthoides</i>	yellow	ww
<i>V. walteri</i> × <i>V. helianthoides</i>	yellow, fading to white	Ww
<i>V. alternifolia</i>	yellow	WWww
<i>V. walteri</i> × <i>V. alternifolia</i>	yellow, fading to white	WWw
<i>V. helianthoides</i> × <i>V. alternifolia</i>	yellow	Www

Thus, the occurrence of a single w allele results in fading florets, whereas two w alleles gives persistently yellow florets. It is therefore reasonable to suggest that *Verbesina walteri* × *V. helianthoides* F₁s, following chromosome doubling, would have the genotype WWww, resulting in persistently yellow florets and plants very similar morphologically to *V. alternifolia*. Similarly, the fading florets of the *V. walteri* × *V. alternifolia* F₁ support the assumption that the white-flowered *V. walteri* is a parental species of *V. alternifolia*. Otherwise, *V. alternifolia* would be wwww, and the Www triploids might be expected to be persistently yellow-flowered.

The available evidence, although not conclusive, strongly suggests that *Verbesina alternifolia* evolved from hybridization between *V. walteri* and *V. helianthoides*, or similar extinct types, followed by spontaneous chromosome doubling in the F₁. Numerous attempts to achieve F₁ chromosome doubling with colchicine have been unsuccessful.

SECTIONAL LIMITS

In their revision of *Verbesina*, Robinson and Greenman (1899) expressed the opinion that many of their sections are artificial. Therefore, the results of the crossing program need to be considered in assessing sectional limits.

Robinson and Greenman treated *Verbesina chapmanii* Coleman (as *V. warei* A. Gray), *V. heterophylla*, and *V. aristata* in sect. *Pterophyton*, *V. helianthoides* in sect. *Verbesinaria*, and *V. walteri* in the genus *Actinomeris*. However, these species, each of which occurs in the eastern United States, can readily be hybridized to produce vigorous, fertile F_1 (Figure 2) and even F_2 and backcross hybrids (Coleman, 1971, 1974). Also, these species are strongly isolated from the remaining species in the program (Figure 1). A more natural treatment would consider these five species, along with *V. alternifolia*, as being consectional. Robinson and Greenman also included *V. rothrockii* and *V. lindheimeri*, both of the southwestern United States and Mexico, in sect. *Pterophyton*. Although these two species demonstrate a strong genetic interrelationship (Figure 2), they are strongly isolated genetically from the eastern species of sect. *Pterophyton* (Figure 1). It is therefore questionable whether they are naturally consectional with the eastern species.

Verbesina occidentalis was treated by Robinson and Greenman in the principally Mexican sect. *Verbesinaria*. Although this species can be successfully crossed with many of the eastern members of sect. *Pterophyton* (Figure 2), the hybrids demonstrate poor chromosome pairing and are highly sterile. However, *V. occidentalis* can readily be crossed with *V. lindheimeri* to form F_1 s with excellent pairing and fair fertility. *Verbesina longifolia* A. Gray, another member of sect. *Verbesinaria*, hybridizes with *V. rothrockii*, again forming F_1 s with excellent pairing and fair fertility (Figure 2). The homology of the chromosomes of *V. occidentalis* and *V. longifolia* with those of *V. lindheimeri* and *V. rothrockii* indicates closer affinities than have previously been suggested.

Verbesina virginica and *V. microptera*, both of sect. *Ochractinia*, demonstrate a close genetic interrelationship and are strongly isolated genetically from the remaining species (Figures 1, 2). *Verbesina encelioides* (Cav.) Benth. & Hook. f. and *V. nana* (Gray) Rob. & Greenm. compose sect. *Ximenesia*, and all attempts to hybridize them have failed (Figure 1).

CROSSING BARRIERS

The principal barrier to the formation of experimental hybrids was failure of interspecific achene formation. The successful germination of hybrid achenes was generally comparable to that of the parent species, and the F_1 generations, with a single exception, were vigorous, as were all F_2 and backcross hybrids grown.

Of the 14 crosses attempted between species which occur or probably occur sympatrically, five (36%) resulted in F_1 s. Of these five F_1 populations, only one (20%) had mean pollen stainability exceeding 20% and 70% or more of the chromosomes associated in bivalents. Of the 41 crosses attempted between species which are probably or clearly allopatric, 16 (39%) yielded F_1 s. Of these 16 F_1 populations 11 (69%) had mean pollen stainability exceeding 50%, and 12 (75%) had 95% or more of the chromosomes associated in bivalents. Thus, although experimental hybridization was equally successful between sympatric and allopatric species, F_1 fertility and chromosome homology were much greater for hybrids formed between allopatric species. Since those species capable of forming fertile F_1 s, thereby permitting the possibility of later generation hybridization and interspecific gene exchange, rarely have contact, the primary reason for the minor role of natural hybridization in the United States species of *Verbesina* is evident.

Even among those species having the possibility of contact, mixed populations are unusual, explaining the rarity of even F_1 s in nature. Spatially isolated species are generally thus maintained by numerous and complex ecological factors. The importance of edaphic factors in the spatial isolation of three northern Florida species has been demonstrated (Coleman, 1974).

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